Arthropoda Selecta 31(2): 183–195

Uralocrangonyx gen.n. (Amphipoda: Crangonyctidae) from the Southern Ural, Russia

Uralocrangonyx gen.n. (Amphipoda: Crangonyctidae) с Южного Урала, Россия

Ivan N. Marin[1], Dmitry M. Palatov[2]
И.Н. Марин[1], Д.М. Палатов[2]

A.N. Severtsov Institute of Ecology and Evolution of RAS, Moscow 119071, Russia.
Институт экологии и эволюции им. А.Н. Северцова РАН, Москва 119071, Россия.
E–mail: coralliodecapoda@mail.ru[1], triops@yandex.ru[2]

KEY WORDS: Diversity, Crustacea, Amphipoda, Crangonyctidae, new genus, subterranean, Southern Ural, Russia.

КЛЮЧЕВЫЕ СЛОВА: Разнообразие, Crustacea, Amphipoda, Crangonyctidae, новый род, подземные, южный Урал, Россия.

ABSTRACT. Integrative analysis revealed that the stygobiotic *Crangonyx chlebnikovi* Borutzky, 1928 (Amphipoda: Crangonyctidae) from the Southern Ural, Russia, should be placed into a separate new genus, *Uralocrangonyx* gen.n. Together with the European *Crangonyx subterraneus* Bate, 1859 and *Crangonyx paxi* Schellenberg, 1935 as well as North American *Bactrurus* spp., the new genus forms the "*Bactrurus*" Clade according to the following morphological features: free urosomites; the dense armature of palm of gnathopods I–II; the absence of sternal gill/processes on pereonal segments II–III; and head with a concave anterolateral lobe bearing moderate inferior antennal sinus. At the same time, the new genus differs from the clade-related genera in the structure and armature of gnathopods I–II and the presence of 8–9 hooks in retinacules of uropods. The erection of this new genus changes the whole taxonomy of the *Crangonyx*-like species, and we propose to resurrect the generic name *Eucrangonyx* Stebbing, 1899 for North American *Crangonyx* sensu lato (with the type species *Eucrangonyx gracilis* (S.I. Smith, 1871)). *Crangonyx islandicus* Svavarsson et Kristjánsson, 2006, endemic to Iceland, should be also allocated into a separate genus, since it is not related to the European *Crangonyx* Spence Bate, 1859 s.str. or any species of the Nearctic *Eucrangonyx* Stebbing, 1899, but belongs to the "*Stygobromus*" clade of the family Crangonyctidae.

How to cite this paper: Marin I.N., Palatov D.M. 2022. *Uralocrangonyx* gen.n. (Amphipoda: Crangonyctidae) from the Southern Ural, Russia // Arthropoda Selecta. Vol.31. No.2. P.183–195. doi: 10.15298/arthsel. 31.2.07

РЕЗЮМЕ. Интегративный анализ показал, что южно-уральский стигобионт *Crangonyx chlebnikovi* Borutzky, 1928 (Amphipoda: Crangonyctidae) должен быть выделен в новый род, *Uralocrangonyx* gen.n. Совместно с европейскими *Crangonyx subterraneus* Bate, 1859 и *Crangonyx paxi* Schellenberg, 1935, а также североамериканскими *Bactrurus* spp., новый род формирует единую кладу "*Bactrurus*" на основании следующих морфологических признаков: свободные уросомиты; мощное вооружение проподуса (ладони) хелипед I–II; отсутствие грудных жабр/отростков на переональных сегментах II–III; и вогнутая переднебоковая доля головы с хорошо выраженным антеннальным синусом. В тоже время, от родственных родов клады новый род хорошо отличается строением (вооружением) обоих хелипед и наличием 8–9 крючков в ретинакулах на уроподах. Выделение нового рода меняет всю таксономическую систему бывшего рода *Crangonyx* sensu lato, и мы предлагаем восстановить род *Eucrangonyx* Stebbing, 1899 для североамериканских видов *Crangonyx* sensu lato (с типовым видом *Eucrangonyx gracilis* (S.I. Smith, 1871)). *Crangonyx islandicus* Svavarsson et Kristjánsson, 2006, эндемичный для Исландии, следует также выделить в отдельный род, поскольку он филогенетически не связан ни с европейским родом *Crangonyx* Spence Bate, 1859 s.str., ни с одним из видов неарктических *Eucrangonyx* Stebbing, 1899, а относится к кладе "*Stygobromus*" семейства Crangonyctidae.

Introduction

The Holarctic family Crangonyctidae (Crustacea: Amphipoda) is represented by a very ancient group of crustaceans that appeared at the end of the Cretaceous in Gondwana [Copilaş-Ciocianu *et al.*, 2019]. Modern representatives of the main clades are scattered across the divergent continents [Kornobis *et al.*, 2011; Copilaş-Ciocianu *et al.*, 2019; Palatov, Marin, 2020; Marin,

Palatov, 2021a]. There are still many unresolved phylogenetic issues concerning the family, which require special attention. Representatives of the genus *Crangonyx* Spence Bate, 1859 are presently known from in North America [Zhang, Holsinger, 2003], Iceland [Svavarsson, Kristjánsson, 2006], Western Europe [Holsinger, Skalski, 1980; Holsinger, 1986; Sidorov *et al.*, 2018], in the Southern Ural [Sidorov *et al.*, 2012], and even Northern Africa (Morocco) [Messouli, 2006]. Central Asian species referring to the genus *Crangonyx* [Holsinger, 1986] were recently moved to the family Gammaridae, mainly to the genus *Tadzocrangonyx* Karaman et Bernard, 1979 [Sidorov *et al.*, 2018].

The type species of the genus *Crangonyx* Spence Bate, 1859, *C. subterraneus* Spence Bate, 1859, was described from a well at Ringwood, Hampshire, South East England [Bate, 1859], while currently it is known from many locations in the south of England [Holsinger, 1986; Johns *et al.*, 2015; Durkota *et al.*, 2019] and northwestern Europe (Northern France, Netherlands, Germany, Switzerland and Luxemburg) [Stock, 1961, 1962; Hoffmann, 1962; Holsinger, Skalski, 1980; Holsinger, 1986; Citoleux, 2007; Alther *et al.*, 2017; Sidorov *et al.*, 2018]. The occurrence of the species in Czech Republic and Poland [Berezina, Ïuriš, 2008; Sidorov *et al.*, 2018] are suspicious as no descriptions or genetic data have been published. *Eucrangonyx vejdovskyi* Stebbing, 1899 and *Niphargus moniezi* Wrzesniowski, 1890 are junior synonyms of this species [Horton *et al.*, 2021].

Nearctic species of the genus *Crangonyx* are represented by about 50 species, distributed in North America [Zhang, Holsinger 2003; Horton *et al.*, 2021]. Stebbing [1899] proposed to allocate a separate genus *Eucrangonyx* Stebbing, 1899 for *Crangonyx gracilis* S.I. Smith, 1871, known from Ontario, Canada. To date, this generic name is reduced to a junior synonym to the genus *Crangonyx*.

Crangonyx islandicus Svavarsson et Kristjánsson, 2006 is endemic to Iceland [Svavarsson, Kristjánsson 2006; Kornobis *et al.*, 2011, 2012], while *Crangonyx africanus* Messouli, 2006 is only known from Morocco, Northern Africa [Messouli, 2006]. There is some doubt that the latter species belongs to the family Crangonyctidae.

Crangonyx paxi Schellenberg, 1935 is known only from a small pond of the Stolni mine in the Klesnica Valley in Sudetenland (western Poland) [Schellenberg, 1935, 1942]. Its taxonomic position was debated, but finally Holsinger & Skalski [1980] came to conclusion that *C. paxi* is a separate species, a deviant representative of the genus *Crangonyx*.

Finally, *Crangonyx chlebnikovi* Borutzky, 1928 was described from the Great Mechka Cave [Borutzky, 1928], while its subspecies, *Crangonyx chlebnikovi maximovitshi* Pankov et Pankova, 2004 was found in the neighboring Kungur (Ice) Cave, Kungur District, the Southern Ural, Russia [Pankov, Pankova, 2004]. Sidorov *et al.* [2010] indicated that this species is related to North-American genus *Bactrurus* Hay, 1902.

In this article, we represent a complete morphological description and molecular genetic data of the representatives of the genus *Crangonyx* s.l. from the Southern Ural, as well as with a discussion on the known distribution and taxonomic position within the family.

Material and methods

Amphipods were collected with a hand net in various cave (subterranean) water resources in the Kungur District, Perm Krai, the Southern Ural, Russia (see Fig. 1). Totally, amphipods were found in three different but neighboring caves, namely the Great Mechna Cave (57°36′36.0″N 56°37′13.0″E) (the type locality of *Crangonyx chlebnikovi* Borutzky, 1928), the Kungur Ice Cave (57°26′28.1″N 57°00′20.9″E) (the type locality of *C. chlebnikovi maximovitshi* Pankov et Pankova, 2004) and the Babinogorskaya Cave (57°27′02.4″N 56°51′32.9″E). After sampling, the specimens were fixed in 90% solution of ethanol.

Photographs were made with a digital camera attached to a Olympus ZX10 and Olympus CX21. The scanning electron microscopic (SEM) images were made using the Vega3 Tescan in the Yu.A. Orlov Paleontological Museum of the Paleontological Institute of the Russian Academy of Sciences, Moscow.

Cytochrome c oxidase subunit I (COI) mtDNA has been proving as extremely informative gene marker in previous studies at both species [Avise, 1993] and higher taxonomic levels [Palatov, Marin, 2020, 2021; Marin, Palatov, 2021a, b]. The COI mtDNA gene marker was amplified with the using of the universal primers LCO1490 (5'–GGTCAACAAATCATAAAGATATTGG–3') and HC02198 (5'–TAAACTTCAGGGTGACCAAAAAATCA–3') [Folmer *et al.*, 1994]. Polymerase chain reaction (PCR) were performed under the standard conditions. Dataset of aligned sequences of COI mtDNA gene markers, about 617 base pairs in length used in the study were taken from the GenBank (NCBI) and author's database.

A consensus of complementary sequences was obtained with MEGA 7.0. The best evolutionary substitution model was determined using MEGA 7.0 and jModeltest2.1.141 as GTR+G+I. A phylogenetic analysis was conducted using PhyML 3.0 (http://www.atgc–montpellier.fr/phyml/) [Guindon *et al.*, 2010] using several models based on BIC (Bayesian Information Criterion) and AIC (Akaike Information Criterion). The phylogenetic trees with a higher bootstrap probability were used for graphically display relationships within the family. Bootstrap support is presented for ML analysis. Pairwise genetic divergences (*p*–distances) was calculated using MEGA 7.0 with the Kimura 2-Parameter (K2P) model of evolution [Kimura, 1980].

The body length (bl., mm), the dorsal length from the distal margin of head to the posterior margin of telson, without uropod III and both antennas, is used as a standard measurement. The type material is deposited in the collection of Zoological Museum of Moscow State University, Moscow, Russia (ZMMU).

Results

PHYLOGENETIC PART. According to the obtained phylogenetic reconstruction (tree) (Fig. 2), *Crangonyx* sensu lato (s.l.) is a polyphyletic group.

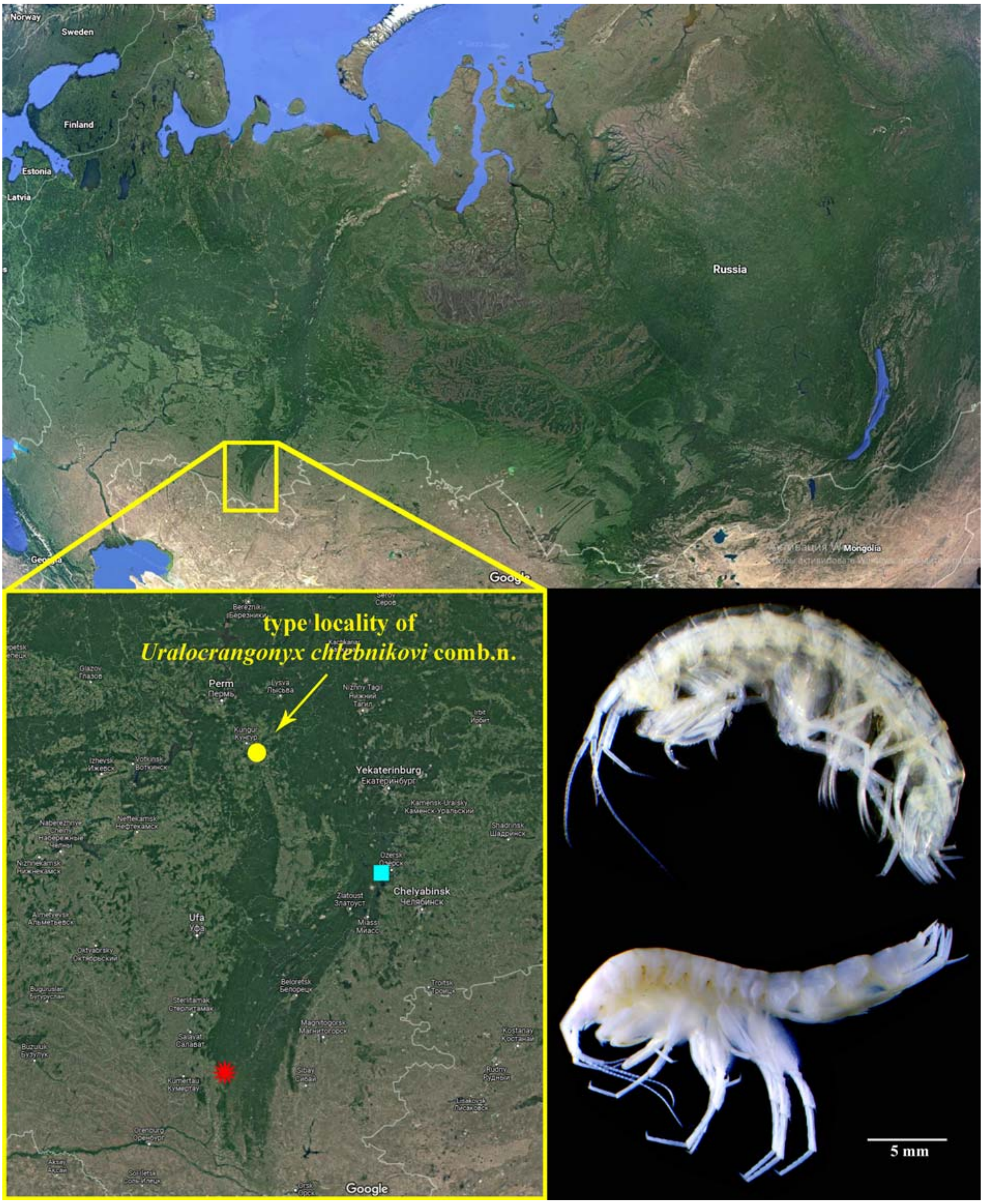


Fig. 1. The map of distribution and general lateral view of *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n. (fixed in ethanol). The red asterisk and blue triangle on the map also show the known (unpublished) records of blind underground crustaceans in the Southern Urals, which presumably belong to the genus *Uralocrangonyx* gen.n.

Рис. 1. Карта распространения и общий вид *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n. (фиксированные в спирте). Красная звездочка и синий треугольник на карте показывают также известные (не опубликовано) находки слепых подземных ракообразных на южном Урале, которые предположительно относятся к роду *Uralocrangonyx* gen.n.

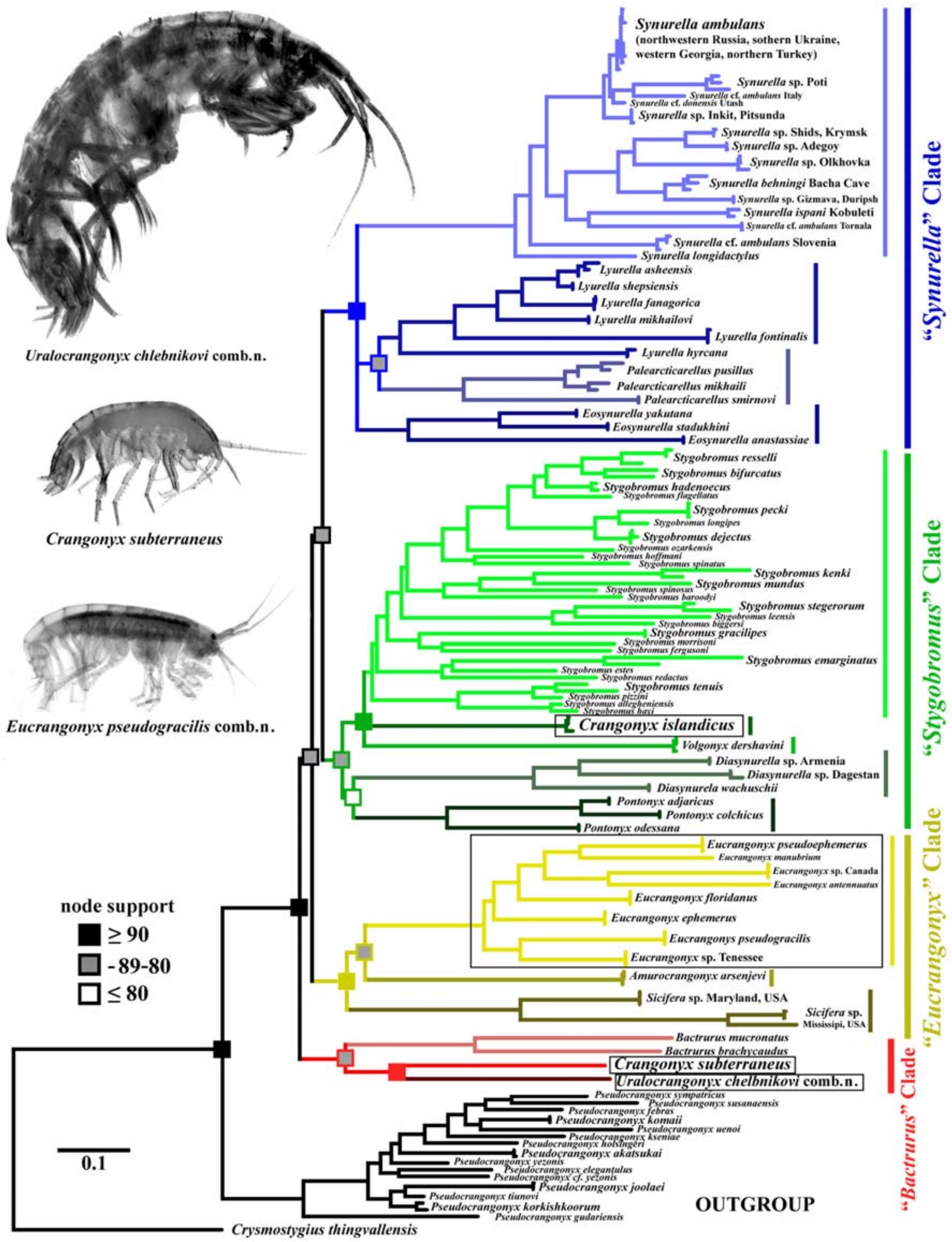


Fig. 2. The phylogenetic reconstruction (tree) of molecular phylogenetic (COI mtDNA gene marker) scenario (GTR+G+I model (AIC)) of the family Crangonyctidae (additional sequences from GenBank (NCBI). Outgroup include species of the genus *Pseudocrangonyx* (Pseudocrangonyctidae) and *Crymostygius thingvallensis* (Crymostygidae).

Photo of *C. subterraneus* by Jules Carter (from https://hcrs.brc.ac.uk/species/crangonyx-subterraneus); *E. pseudogracilis* by Malcolm Storey (from https://www.discoverlife.org/mp/20p?see=I_MWS48333&res=640)

Рис. 2. Филогенетическая реконструкция (дерево) молекулярно-филогенетического сценария (генный маркер COI мтДНК) (модель GTR+G+I (AIC)) семейства Crangonyctidae (дополнительные последовательности взяты из GenBank (NCBI). Аутгруппа представлена видами рода *Pseudocrangonyx* (Pseudocrangonyctidae) и *Crymostygius thingvallensis* (Crymostygidae).

Фото *C. subterraneus* — Жюлес Картер (https://hcrs.brc.ac.uk/species/crangonyx-subterraneus); *E. pseudogracilis* — Малкольм Сторей (https://www.discoverlife.org/mp/20p?see=I_MWS48333&res=640)

The lineage of *C. subterraneus* [Spence Bate, 1859], and possibly *C. paxi*, which is apparently related to *C. subterraneus* [Holsinger, Skalski, 1980], represent the genus *Crangonyx* sensu stricto (s.). The Nearctic *Bactrurus* spp., and two Palaearctic species, the western European *Crangonyx subterraneus* Spence Bate, 1859 (*Crangonyx* s.str.) and *Crangonyx chlebnikovi* Borutzky, 1928 from the Southern Ural, form a well-supported separated clade — the "*Bactrurus*" Clade (see Fig. 2). At the same time, *C. chlebnikovi* represents a well-supported monophyletic lineage separated from *C. subterraneus* (see below), and its designation into a separate genus is well justified.

The North American *Crangonyx* s. l. is phylogenetically separated from the "*Bactrurus*" Clade (see Fig. 2), and we propose to resurrect for it the generic name *Eucrangonyx* Stebbing, 1899, with the type species *Crangonyx gracilis* S.I. Smith, 1871 [Stebbing, 1899]. The Nearctic *Eucrangonyx* spp., *Sicifera* spp. and the Palaearctic *Amurocrangonyx arsenjevi* (Derzhavin, 1927) form a well-supported separate clade — the "*Eucrangonyx*" Clade.

Crangonyx islandicus Svavarsson et Kristjánsson, 2006, endemic to Iceland, is phylogenetically unrelated neither to the European *Crangonyx* s.str. not to the North American *Eucrangonyx*, but belongs to a phylogenetic distinct "*Stygobromus*" Clade (see Fig. 2). Moreover, this species represent a distinct lineage, which should be separated into a new genus.

TAXONOMIC PART

Order Amphipoda Latreille, 1816
Infraorder Gammarida Latreille, 1802
Family Crangonyctidae Bousfield, 1973
Uralocrangonyx **gen.n.**

DIAGNOSIS. Relatively large-sized species amphipod, with males smaller than females, without secondary sexual dimorphism. *Body* unpigmented, smooth. *Eyes* completely reduced. *Head* with moderate inferior antennal sinus. *Laterallia* with 16 strong pectinate setae. *Antenna I* with slender aesthetascs and 2-segmented accessory flagellum. *Pereonal segments* II–III without sternal gill/processes. *Gnathopod I* smaller than GnII, both with teardrop-shaped propodus (palm); ventral palmar margin with deep ventroproximal cavity and armed with two deep rows of notched robust setae (teeth) along the entire length. *Pleon* with free urosomites. *Pleopods* with 8 hooks in retinacules in both sexes. *Uropod III* with outer ramus about 3 times as long as wide, rather wide, with several clusters of marginal and a tuft of distal setae. *Telson* entire, rectangular, wider than long, with marginal clusters of spines.

DIFFERENTIAL DIAGNOSIS. The new genus clearly belongs to the aforementioned phylogenetic "*Bactrurus*" Clade (including North American genus *Bactrurus* and European *Crangonyx* s.str. (*C. subterraneus* + *C. paxi*)), which is characterized by: 1) head with an anterolateral sinus; 2) free urosomites; 3) teardrop-shaped form and the armature of palm (propodi) of gnathopods I–II with the entire ventral margin armed with 2 rows of notched robust setae; and 4) the absence of sternal gill/processes on pereonal segments II–III. The characteristic combination of these morphological features clearly separates these genera from other crangonyctids. *Crangonyx paxi* is a poorly described species, known by immature specimens, it possibly related to *C. subterraneus* according to numerous morphological features [Holsinger, Skalski, 1980] as well as the presence of only 2 hooks in retinacules of pleopods. We consider this species within the genus *Crangonyx* s.str.

Uralocrangonyx chlebnikovi (Borutzky, 1928) comb.n. is the only species within the "*Bactrurus*" clade that possesses 8 hooks in the retinacules of pleopods (vs. 2 hooks in *Bactrurus* and *Crangonyx* s.str.). Such feature is the most striking diagnostic feature of the species and the new genus. A large number of hooks (more than 4) is possibly an ancestral feature [Marin, Palatov, 2021]. However, this new genus can be also separated from *Bactrurus* by a long (about 3 times as long as wide) outer ramus of uropod III (vs. about 1–1.5 times as long as wide in *Bactrurus* and *Crangonyx* s.str.); specific teardrop-shaped palm of gnathopods I–II with deep ventroproximal cavity and ventral palmar margin armed with 2 deep rows of notched robust setae (teeth) along the entire length in *Uralocrangonyx* gen.n also well morphologically separates the new genus from *Crangonyx* s.str. (vs. mostly rectangular palm with oblique palmar margin with armed with bifurcate robust setae only distal margin and without ventroproximal cavity in *Crangonyx* s.str.). Also, representatives of the genus are among the largest in this clade, with females reaching 20 mm in length [Borutzky, 1928; Sidorov *et al*., 2012], similar to the genus *Bactrurus,* reaching 20 mm [Koenemann, Holsinger, 2001]. Representatives of *Crangonyx* s.str does not exceed 7 mm in length [Holsinger, Skalski, 1980].

The new can be clearly separated from all Palaearctic crangonyctid genera by 1) head with a well-marked anterolateral sinus (vs. distally rounded); 2) laterallia with 16 strong pectinate setae (vs. 10 setae in *Pontonyx* Palatov et Marin, 2021, 10–13 — in *Amurocrangonyx* Sidorov et Holsinger, 2007 and 8 — in all genera from the "*Synurella*" Clade (see Fig. 2); 3) teardrop-shaped palm of gnathopods I–II with deep ventroproximal cavity and ventral palmar margin armed with 2 deep rows of notched robust setae (teeth) along the entire length; 4) the absence of sternal gill/processes on pereonal segments II–III; 5) 8–9 hooks in the retinacules of pleopods (vs. less than 4 hooks in other Palaearctic crangonyctid genera with the exception of *Volgonyx* Marin et Palatov, 2021 bearing 8–9 hooks in the retinacules); 6) relatively slender basis of ambulatory pereiopods, especially PVII; and 7) large outer ramus of uropod III, which is about 3 times as long as wide.

ETYMOLOGY. The genus is named after the region where it is distributed, the Southern Ural; the meaning is "*Crangonyx* from Ural".

Uralocrangonyx chlebnikovi (Borutzky, 1928) **comb.n.**
Figs 3–8.

Crangonyx chlebnikovi Borutzky, 1928

Crangonyx chlebnikovi maximovitshi Pankov et Pankova, 2004

MATERIAL EXAMINED. Russian Federation, Southern Ural, Perm Krai, Kungur District: 1♀ (bl. 16.5 mm) (ZMMU Mb-1220), 7♀♀ (bl. 16–19 mm) (LEMMI), Kungur Ice Cave, 57°26′28.1″N 57°00′20.9″E, in subterranean lake, 12.07.2020; 3♀♀ (bl. 16.0–16.5 mm), Great Mechna, 57°36′36.0″N 56°37′13.0″E, in subterranean lake, coll. O.I. Kadebskaya, 20.09.2017; 4♀♀ (bl. 16–19 mm), Kungur Ice Cave, in subterranean lake, coll. O.I. Kadeb-

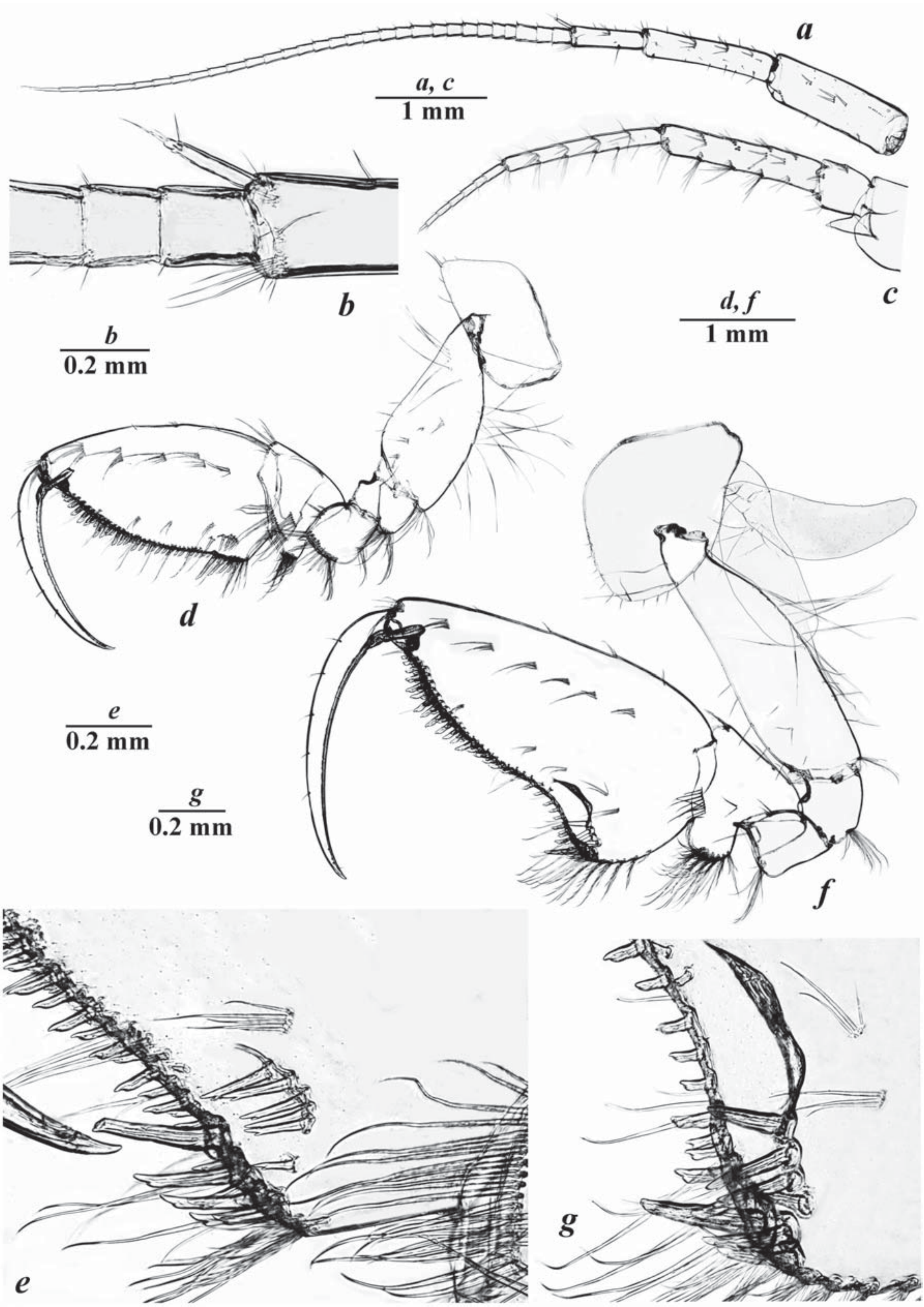


Fig. 3. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — antenna I; *b* — accessory flagellum of antenna I; *c* — antenna II; *d* — gnathopod I; *e* — distoventral corner of chela of GnI; *f* — gnathopod II; *g* — distoventral corner of chela of GnII.

Рис. 3. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — антенна I; *b* — дополнительный жгутик антенны I; *c* — антенна II; *d* — гнатопод I; *e* — дистовентральный угол клешни GnI; *f* — гнатопод II; *g* — дистовентральный угол клешни GnII.

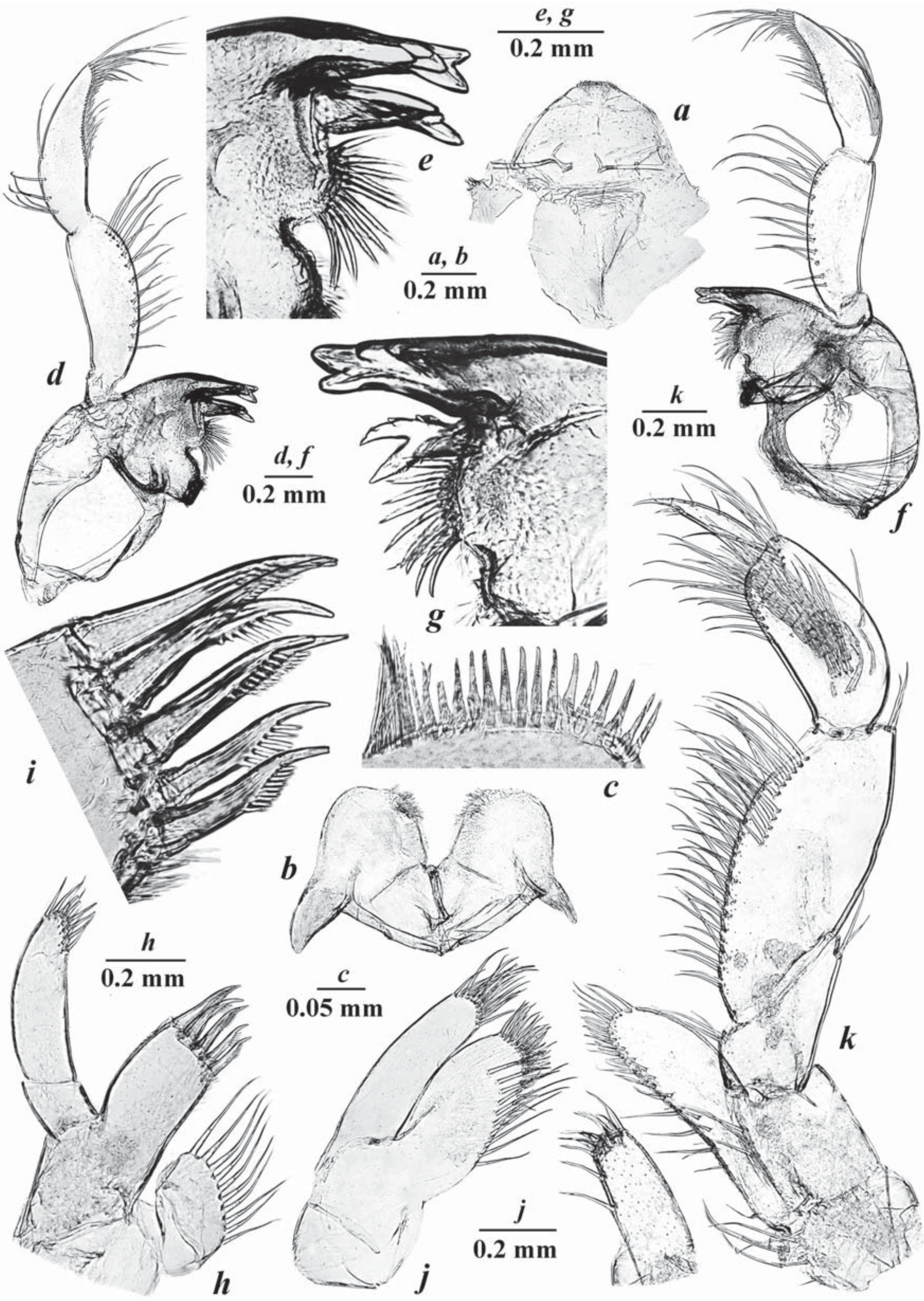


Fig. 4. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — labrum (upper lip); *b* — labium (lower lip); *c* — lateralia; *d*, *f* — mandible; *e*, *g* — incisor process and pars incisiva of mandible; *h* — maxilla I; *i* — same, distal margin of outer lobe; *j* — maxilla II; *k* — maxilliped.

Рис. 4. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — верхняя губа; *b* — нижняя губа; *c* — латералия; *d*, *f* — мандибула; *e*, *g* — режущий отросток и pars incisiva (резец) мандибулы; *h* — максилла I; *i* — то же, дистальный край наружной доли; *j* — максилла II; *k* — максиллипед.

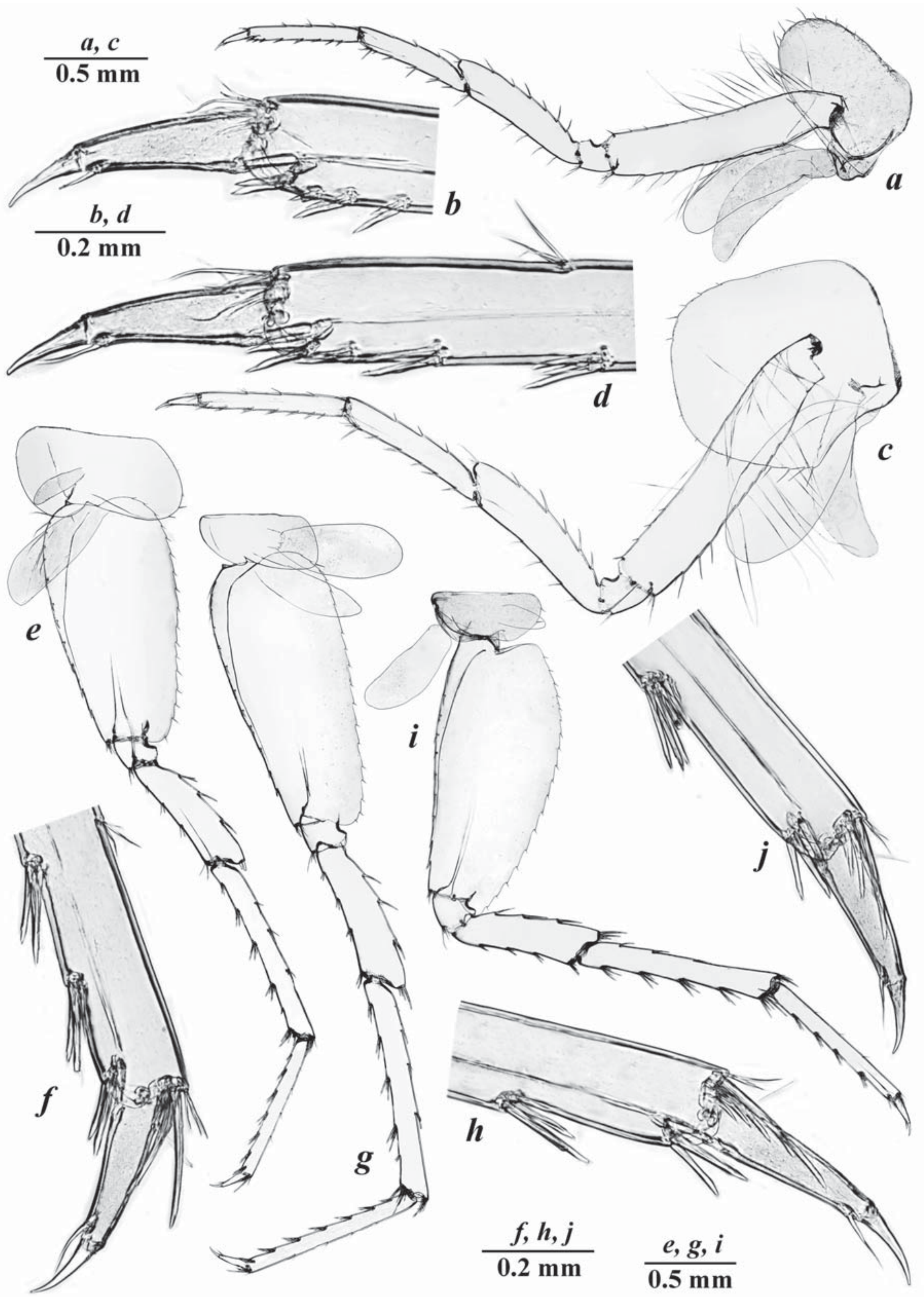


Fig. 5. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — pereopod III; *b* — dactylus of PIII; *c* — pereopod IV; *d* — dactylus of PIV; *e* — pereopod V; *f* — dactylus of PV; *g* — pereopod VI; *h* — dactylus of PVI; *i* — pereopod VII; *j* — dactylus of PVII.

Рис. 5. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — переопода III. *b* — дактилус PIII; *c* — переопода IV; *d* — дактилус PIV; *e* — переопода V; *f* — дактилус PV; *g* — переопода VI; *h* — дактилус PVI; *i* — переопода VII; *j* — дактилус VII.

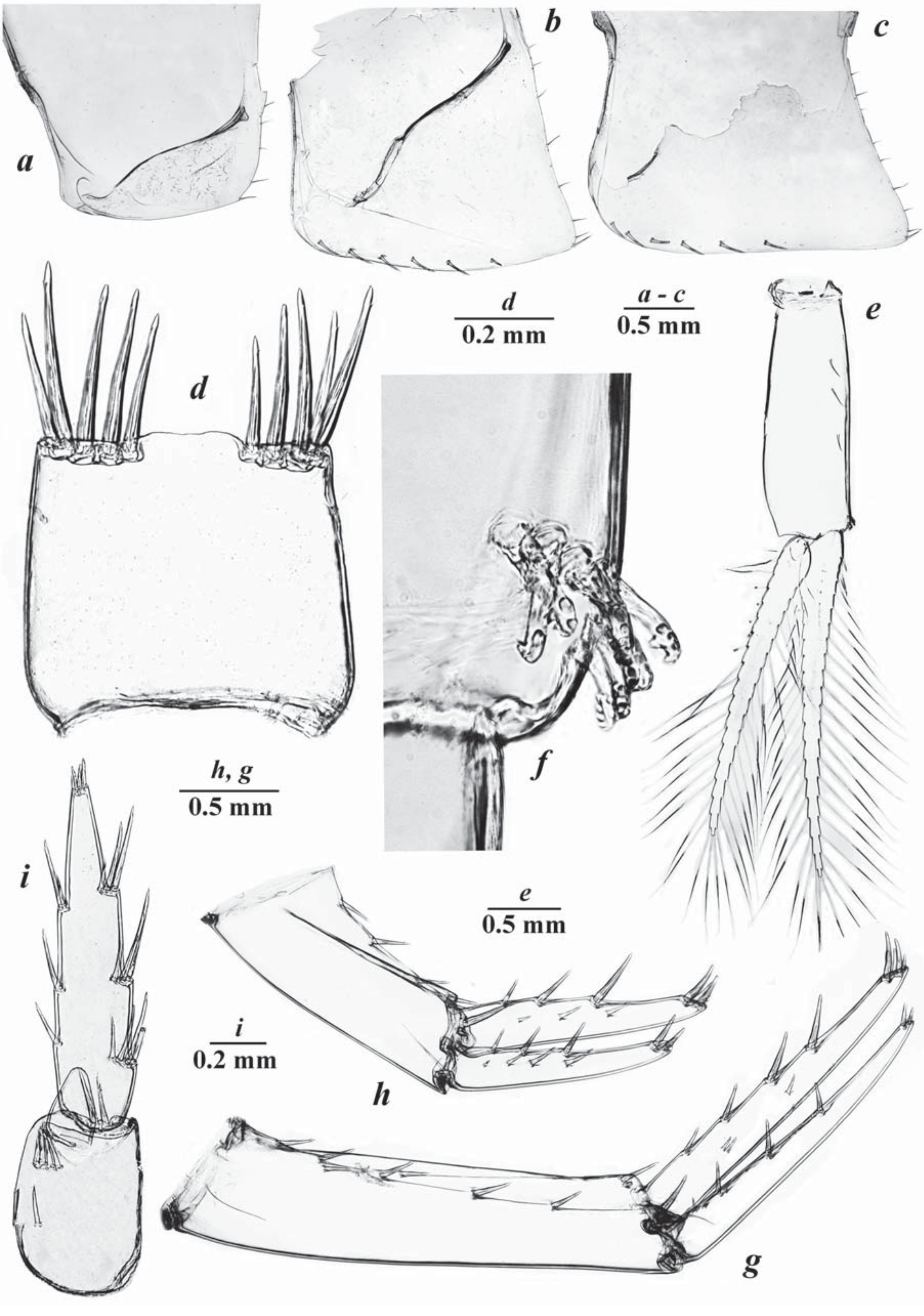


Fig. 6. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a–c* — epimeral plates I–III; *d* — telson; *e* — pleopod III; *f* — retinacula of pleopod III; *g* — uropod I; *h* — uropod II; *i* — uropod III.

Рис. 6. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a–c* — эпимеральные пластинки I–III; *d* — тельсон; *e* — плеопода III; *f* — ретинакула плеоподы III; *g* — уропода I; *h* — уропода II; *i* — уропода III.

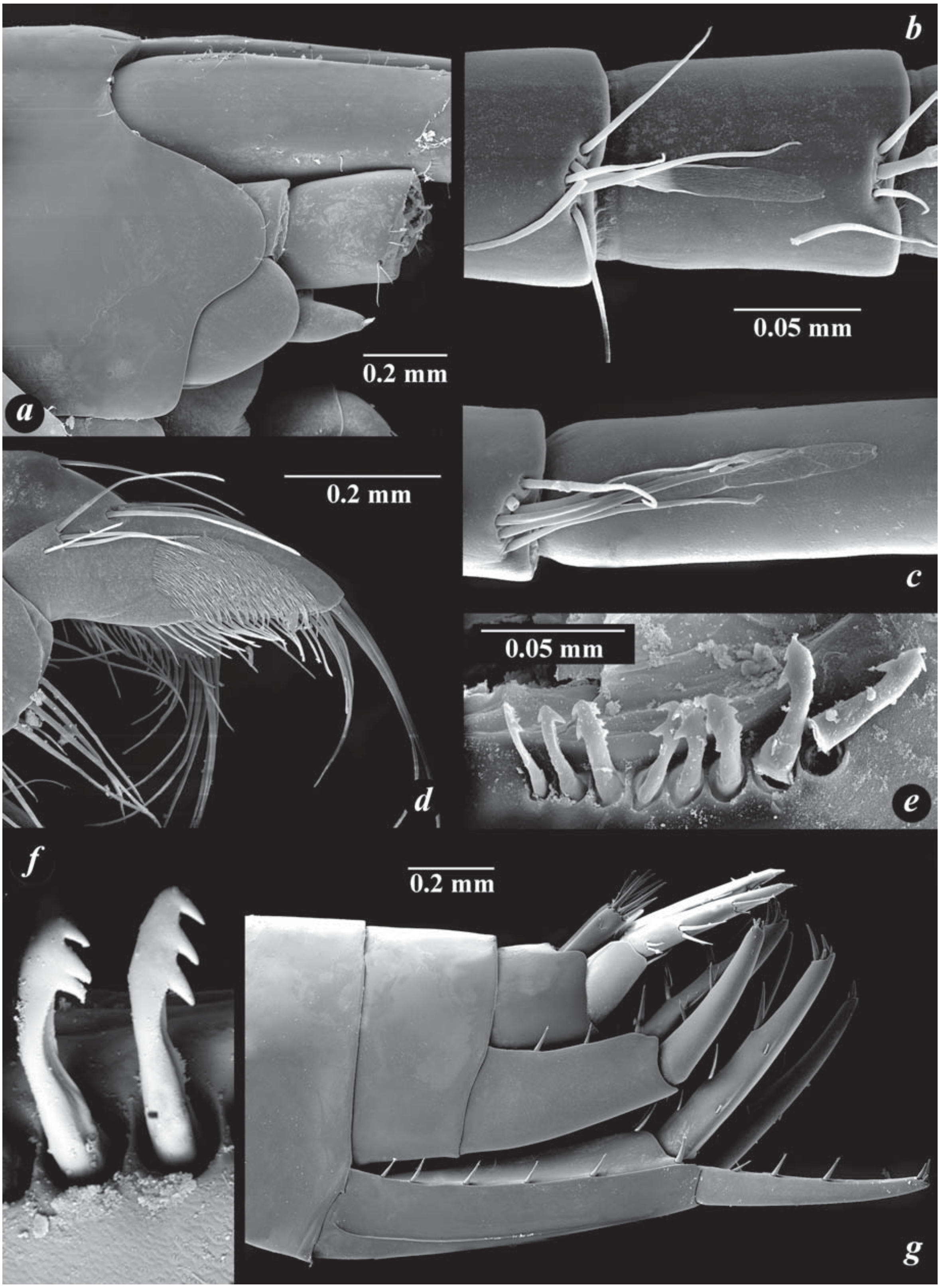


Fig. 7. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — head; *b*, *c* — aesthetascs of antenna I; *c* — antenna II; *d* — distal segment of mandibular palp; *e* — retinacula of pleopod I; *f* — hooks of retinacula; *g* — urosomal segments.

Рис. 7. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — голова; *b*, *c* — эсцетаски антенны I; *c* — антенна II; *d* — дистальный сегмент щупика мандибулы; *e* — ретинакула плеоподы I; *f* — крючки ретинакулы; *g* — уросомальные сегменты.

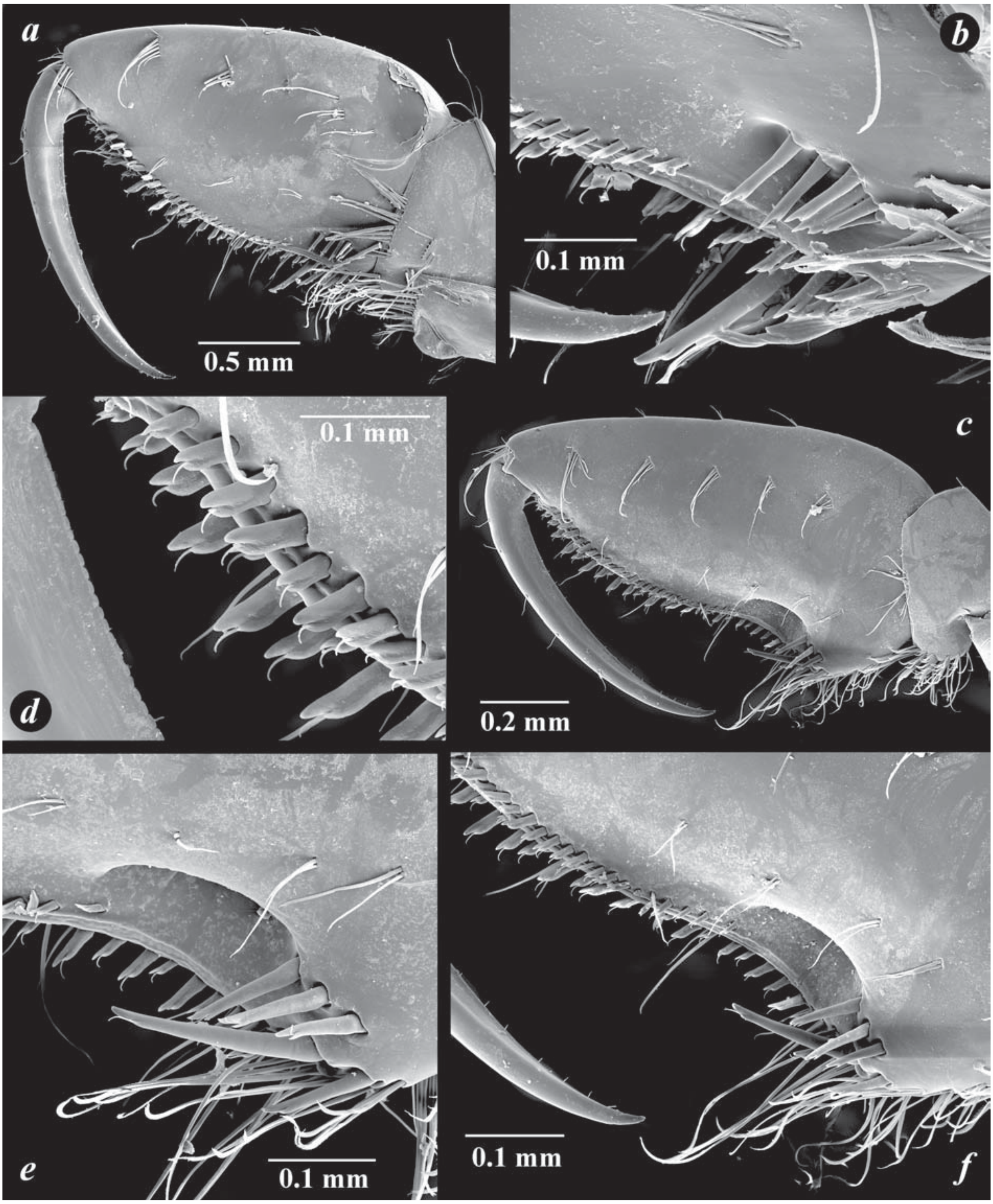


Fig. 8. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — palm (chela) of gnathopod I; *b* — proximoventral margin of palm of GnI; *c* — palm (chela) of gnathopod II; *d* — distoventral margin of palm (chela) and cutting margin of dactylus of GnII; *e*, *f* — proximoventral margin of palm (chela) of GnII.

Рис. 8. *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n., ♀: *a* — ладонь (клешня) гнатоподы I; *b* — проксимовентральный край ладони GnI; *c* — ладонь (клешня) гнатоподы II; *d* — дистовентральный край ладони и режущий край дактилюса GnII; *e*, *f* — проксимовентральный край ладони GnII.

skaya, 2.09.2017; 1♀ (bl. 16.0 mm) (ZMMU Mb-1221), 3♀♀ (bl. 15–15.5 mm) (LEMMI), Babinogorskaya Cave, 57°27′02.4″N 56°51′32.9″E, in subterranean lake, coll. O.I. Kadebskaya, 2.09.2017.

DIAGNOSIS. As for the genus (see above).

REMARKS. The species is well described by Sidorov *et al.* [2012], while the lectotype of the species in deposited in ZMMU (Tb-1114) [Sidorov *et al.*, 2012]. The specimens examined in this study fully correspond to the original and subsequent descriptions of the species (see Figs 3–6).

DISTRIBUTION AND ECOLOGY. Stygobiotic species, which is known from cave (subterranean) water reservoirs and wells of Kungur, Orda and Suksun districts of Perm Krai, the Southern Ural, Russia (Fig. 1) [Sidorov *et al.*, 2012].

Discussion

Recently, the taxonomic structure of the family Crangonyctidae has undergone a serious revision, mainly due to the possibility of using molecular genetic methods [Kornobis *et al*., 2011; Copilaş-Ciocianu *et al*., 2019; Marin, Palatov, 2021]. A number of new genera were erected for previously described species [Sidorov, Holsinger, 2007; Palatov, Marin, 2020; Marin, Palatov, 2021a; Cannizzaro *et al*., 2021]. Our article continues this series of taxonomic publications and most likely offers a final solution for the distribution of known genera into the main clades of the family, although probably some taxonomic changes are still possible.

At the same time, we believe that the diversity of crangonyctid amphipods in the Palaearctic is still poorly understood, and the diversity of the genus *Uralocrangonyx* gen.n. is still underestimated. For example, there were several reports on blind cave crustaceans near Ufa in Bashkiria and Chelyabinsk region, the Southern Ural (see Fig. 1). Such records from areas distantly remote from the type locality of *Uralocrangonyx chlebnikovi* (Borutzky, 1928) comb.n. in the Perm region, with high probability belong to another species of the genus, obviously new to science.

Currently, more than 50 species of *Eucrangonyx* and 130 species of *Stygobromus* have been discovered in the Nearctic [Cannizzaro, Savicki, 2019; Gibson *et al*., 2021; Cannizzaro *et al*., 2021]. At the same time, taking into account the inequality of known crangonyctid across the Palearctic and even Russia, the endemicity of many species (for example, *Lyurella* spp. in the Caucasus [Marin, Palatov, 2021b] or *Pontonyx* spp. in the Colchis Lowland [Marin, Palatov, 2021a]) and genera with a narrow distribution (for example, *Volgonyx* Marin et Palatov, 2021 in Saratov region [Marin, Palatov, 2021a]), as well as an even larger unexplored territory, it is safe to say that the diversity of the family in the Palaearctic is still far from being completely studied, probably even at the generic level.

Moreover, the study of underestimated diversity in the Palearctic can significantly change the presented concept of the origin and distribution of the family Crangonyctidae [Copilaş-Ciocianu *et al.*, 2019, 2020]. Three of four main clades of the family (Fig. 2) includes representatives in both Nearctic and Palaearctic, while the “*Synurella*” Clade is represented only by Palaearctic species, and their diversity has not yet been fully studied [Palatov, Marin, 2020, 2021; Marin, Palatov, 2021a, b]. We hope that a more detailed study of all species of the family using integrative approach will allow in the future to provide a more detailed revision of the family and revising the issues of its origin.

Conflict of Interests

The authors declare no potential conflict of interest.

Acknowledgements. The authors are sending their special thanks to Ilya Turbanov (Borok) and Olga I. Kadebskaya (Perm), who provided an additional material from the Kungur Ice, the Great Mechna and the Babinogorskaya caves, the Southern Ural, Russia; and to Ph.D. student Andrew Cannizzaro (Miami University), who kindly reviewed manuscript and offered substantial and valuable comments. The study is supported by the Russian Foundation for Basic Research (RFBR) (grant No. 20-04-00803_A).

References

Alther R., Švara V., Fišer C., Altermatt F. 2017. Amphipods of Switzerland // The 17th International Colloquium on Amphipoda, Trapani (Italia), 4–7 September 2017. P.585–586.

Bate C.S. 1859. On the genus *Niphargus* (Schiödte) // Proceedings of the Dublin University Zoological and Botanical Association. Vol.1. P.237–240.

Berezina N., Ďuriš Z. 2008. First record of the invasive species *Dikerogammarus villosus* (Crustacea: Amphipoda) in the Vltava River (Czech Republic) // Aquatic Invasions. Vol.3. No.4. P.455–460. http://doi.org/10.3391/ai.2008.3.4.16

Borutzky E.V. 1928. Materialien über die Fauna der unterirdischen Gewässer: *Crangonyx chlebnikovi* sp. n. (Amphipoda) aus den Höhlen des mittleren Urals // Zoologischer Anzeiger. Bd.77. S.253–259.

Cannizzaro A.G., Sawicki T.R. 2019. Two new species of the genus *Crangonyx* Bate, 1859 (Amphipoda: Crangonyctidae) from the St. Marks River Basin with notes on the ‘*Crangonyx floridanus* complex’ // Zootaxa. Vol.4691. P.301–332. https://doi.org/10.11646/zootaxa.4691.4.1

Cannizzaro A.G., Daniels J.D., Berg D.J. 2021. Phylogenetic analyses of a new freshwater amphipod reveal polyphyly within the Holarctic family Crangonyctidae, with revision of the genus *Synurella* // Zoological Journal of the Linnean Society. zlab092. https://doi.org/10.1093/zoolinnean/zlab092

Citoleux J. 2007. Contribution à la connaissance des Crustacés Amphipodes stygobies du Finistère // Invertébrés Armoricains. Vol.1. P.41–43.

Copilaş-Ciocianu D., Sidorov D.A., Gontcharov A. 2019. Adrift across tectonic plates: molecular phylogenetics supports the ancient Laurasian origin of old limnic crangonyctid amphipods // Organisms Diversity & Evolution. https://doi.org/10.1007/s13127–019–00401–7

Durkota J.M., Wood P.J., Johns T., Thompson J.R., Flower R.J. 2019. Distribution of macroinvertebrate communities across surface and groundwater habitats in response to hydrological variability // Fundamental and Applied Hydrobiology. https://doi.org/10.1127/fal/2019/1156

Gibson R., Hutchins B.T., Krejca J.K., Diaz P.H., Sprouse P.S. 2021. *Stygobromus bakeri*, a new species of groundwater amphipod (Amphipoda, Crangonyctidae) associated with the Trinity and Edwards aquifers of central Texas, USA // Subterranean Biology. Vol.38. P.19–45. https://doi.org/10.3897/subtbiol.38.61787

Hoffmann J. 1962. Faune des Amphipodes du Grand-Duché de Luxembourg // Archives de la Section des Sciences de l'Institut Grand-Ducal, Nouvelle Série. Vol.29. P.1–128.

Holsinger J.R. 1986. Holarctic crangonyctid amphipods // Botosaneanu L. (ed.). Stygofauna Mundi. Leiden: Brill. P.535–549.

Holsinger J.R., Skalski A.W. 1980. The taxonomy and systematic status of *Crangonyx paxi* Schellenberg (Crangonyctidae) // Crustaceana. Suppl.6. P.17–26.

Horton T., Lowry J., De Broyer C., Bellan-Santini D., Coleman C.O., Corbari L., Costello M.J., Daneliya M., Dauvin, J.-C., Fišer C., Gasca R., Grabowski M., Guerra-García J.M., Hendrycks E.; Hughes L., Jaume D., Jazdzewski K., Kim Y.-H., King R., Krapp-Schickel T., LeCroy S., Lörz A.-N., Mamos T., Senna A.R., Serejo C., Sket B., Souza-Filho J.F., Tandberg A.H., Thomas J.D., Thurston M., Vader W., Väinölä R., Vonk R., White K., Zeidler W. 2021. World Amphipoda Database. *Crangonyx* Spence Bate, 1859. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=431462 on 2021–12–18

Johns T., Jones J.I., Knight L., Maurice L., Wood P., Robertson A. 2015. Regional-scale drivers of groundwater faunal distributions // Freshwater Science. Vol.34. No.1. P.316–328. https://doi.org/10.1086/678460

Marin I., Palatov D. 2021a. *Volgonyx* gen.n. and *Pontonyx* gen.n., two new genera of the family Crangonyctidae (Crustacea: Amphipoda) from the southeastern Europe // Arthropoda Selecta. Vol.30. No.1. P.43–61. https://doi.org/10.15298/arthsel.30.1.05

Marin I.N., Palatov D.M. 2021b. The hidden diversity of the genus *Lyurella* Derzhavin, 1939 (Crustacea: Amphipoda: Crangonyctidae): four new species from the subterranean habitats of the northwestern Caucasus, Russia // Zootaxa. Vol.5006. No.1. P.127–168. https://doi.org/10.11646/zootaxa.5006.1.17

Messouli M. 2006. The first African Crangonyctidae, *Crangonyx africanus* nov. sp. (Crustacea Amphipoda) in the groundwaters of Western Morocco: systematics and biogeographical implications // Subterranean Biology. Vol.4. P.67–78.

Koenemann S., Holsinger J.R. 2001. Systematics of the North American subterranean amphipod genus *Bactrurus* (Crangonyctidae) // Beaufortia. Vol.51. No.1. P.1–56.

Kornobis E., Pálsson S., Sidorov D.A., Holsinger J.R., Kristjánsson B.K. 2011. Molecular taxonomy and phylogenetic affinities of two groundwater amphipods, *Crangonyx islandicus* and *Crymostygius thingvallensis*, endemic to Iceland // Molecular Phylogenetics and Evolution. Vol58. No.3. P.527–539. https://doi.org/10.1016/j.ympev.2010.12.010

Kornobis E., Pálsson S., Svavarsson J. 2012. Classification of *Crangonyx islandicus* (Amphipoda, Crangonyctidae) based on morphological characters and comparison with molecular phylogenies // Zootaxa. Vol.66. No.3233. P.52–66. https://doi.org/10.1099/ijs.0.047324–0

Palatov D.M., Marin I.N. 2020. A new genus of the family Crangonyctidae (Crustacea, Amphipoda) from the Palaearctic, with descriptions of two new species from the foothills of the Altai mountains // Zoologicheskyi Zhurnal. Vol.99. No.10. P.1160–1186. https://doi.org/10.31857/S004451342010013X

Palatov D.M., Marin I.N. 2021. When males and females belong to different genera: an interesting case of *Synurella/Pontonyx* (Crustacea: Amphipoda: Crangonyctidae) co-occurrence // Arthropoda Selecta. Vol.30. No.4. P.443–472. https://doi.org/10.15298/arthsel.30.4.03

Pankov N.N., Pankova N.V. 2004. [The biology of the cave amphipod, *Crangonyx chlebnikovi* Borutzky, 1928 (Gammaridae), with the description of new subspecies from Kungur Ice Cave] // Peshchery: mezhvuzovskiy sbornik nauchnykh trudov. Perm: Perm University. Vol.29–30. P.141–149 [in Russian].

Schellenberg A. 1935. Die Höhlenfauna des Glatzer Schneeberges, 2. Höhlenamphipoden des Glatzer Schneeberges // Beiträge zur Biologie des Glatzer Schneeberges. Bd.1. S.72–75.

Schellenberg A. 1942. Flohkrebse oder Amphipoda // Die Tierwelt Deutschlands. Bd.46. S.1–252.

Sidorov D.A., Holsinger J.R. 2007. *Amurocrangonyx*, a new genus of subterranean amphipod (Crangonyctidae) from the Russian Far East, with a redescription of the poorly known *Crangonyx arsenjevi* and comments on biogeographic relationships // Journal of Crustacean Biology. Vol.27. No.4. P.660–669. https://doi.org/10.1651/s-2817r.1

Sidorov D.A., Pankov N.N., Krasheninnikov A.B. 2010. A *Bactrurus*-like subterranean amphipod (Crangonyctidae) from the Ural Mountain karst region // XX International Conference of Subterranean Biology: Abstract book. Postojna, Slovenia. P.145.

Sidorov D.A., Pankov N.N., Holsinger J.R. 2012. Distribution and ecology of the subterranean amphipod *Crangonyx chlebnikovi* Borutzky, 1928 (Crustacea: Crangonyctidae), with lectotype designation and comments on morphology of the lateral cephalic lobe // Arthropoda Selecta. Vol.21. No.2. P.149–160. https://doi.org/10.15298/arthsel.21.2.04

Sidorov D., Hou Z., Sket B. 2018. Three new remarkable amphipod species (Crustacea: Gammaridae) from springs and subterranean waters of Central Asia // Zootaxa. Vol.4444. No.4. P.437. https://doi.org/10.11646/zootaxa.4444.4.

Smith S.I., Verrill A.E. 1871. Notice of the Invertebrata dredged in Lake Superior in 1871 by the US Lake Survey under the direction of Gen. CB Comstock, SI Smith, naturalist // American Journal of Science and Arts. Vol.3. No.2. P.448–454.

Stock J.H. 1961. Ondergrondse waterdieren in Zuid-Limburg // Natuurhistorisch Maandblad Limburg. Bd.50. No.7–8. S.77–85.

Stock J.H. 1962. Animals from pump-water in Geulhem (South Limburg) // Natuurhistorisch Maandblad Limburg. Bd.51. No.3. P.38.

Svavarsson J., Kristjánsson B.K. 2006. *Crangonyx islandicus* sp. nov., a subterranean freshwater amphipod (Crustacea, Amphipoda, Crangonyctidae) from springs in lava fields in Iceland // Zootaxa. Vol.1365. P.1–17. https://doi.org/10.11646/zootaxa.1365.1.1

Zhang J., Holsinger J.R. 2003. Systematics of the freshwater amphipod genus *Crangonyx* (Crangonyctidae) in North America // Virginia Museum of Natural History, Memoir. Vol.6. P.1–274. https://doi.org/10.25777/s8tw-2q09

Responsible editor K.G. Mikhailov